

# The Fluid Dynamical Context of Chemosensory Behavior

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**Abstract.** The fluid mechanical environment provides the context in which denizens of aquatic realms, as well as terrestrial creatures, use chemoperception to search for objects. Our ability to understand the nature of olfactory-guided navigation rests on our proficiency at characterizing the fluid dynamic setting and at relating properties of flow to behavioral and sensory mechanisms. This work reviews some fluid dynamical concepts that are particularly useful in describing aspects of flow relevant to chemosensory navigation, and it considers studies of orientation in animals in light of these principles. Comparisons across broadly different fluid environments suggest that particular sensory and behavioral mechanisms may be tailored to specific flow regimes and stimulus environments. This is clearly evident when examining animals that operate in high vs. low Reynolds number flows. In other cases, animals may converge on common solutions in given flow regimes in spite of differences in taxonomic class or size. Potential parallels may include behavior of aquatic vs. terrestrial arthropods, and animals without fixed reference points in flows dominated by molecular vs. turbulent diffusion. In an effort to add further fluid dynamical underpinnings to navigational strategies, I suggest how simple nondimensional categorization of behavior in relation to flow may aid in identifying the forces underlying common elements, even across animals of seemingly disparate size and scale.

## Introduction

Aquatic animals rely on chemosensory abilities for nearly every task necessary for their survival, although we, as

terrestrial animals, may have difficulty appreciating the information that they are able to obtain. Nonetheless, habitat choice (Pawlik, 1992; Zimmer-Faust and Tamburri, 1994; Ratchford and Eggleston, 1998), prey perception (Koehl and Strickler, 1981; Weissburg and Zimmer-Faust, 1993, 1994), predator avoidance (Kats and Dill, 1998), and mating (Gleeson, 1982; Kelley *et al.*, 1998; Yen *et al.*, 1998) have all been shown to be strongly associated with chemical cues in a variety of organisms. Even a brief survey of chemical communication systems suggests that over ecological and evolutionary time spans, chemical signaling processes affect individual organisms from the microscopic to the macroscopic, as well as their populations and communities (Zimmer and Butman, 2000).

In the last decade, great strides have been made in understanding the role of chemosensory cues in the marine and freshwater communities. The initial focus on identifying the sources and molecular nature of chemical cues, and their behavioral effects, has given way to efforts to understand the spatial and temporal properties of chemical signals. This shift occurred in response to the realization that the properties of fluids and fluid motion play a pivotal role in structuring chemical signals available to aquatic organisms. Various studies suggest that the fluid dynamical regime sets boundary conditions on behavioral abilities through its effects on the information contained in the odor signal (Moore and Atema, 1991; Weissburg and Zimmer-Faust, 1993, 1994; Weissburg *et al.*, 1998). The clear conclusion from these investigations is that the hydrodynamic context of chemosensory behavior is an important component of the animal's chemical environment.

The purpose of this contribution is to give a broad overview of the effects of hydrodynamic forces on the nature of waterborne chemical signals; such an overview is necessarily rooted in an appreciation of fluid dynamic regimes. At this nascent stage of our investigations, a relatively simple

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approach can serve to outline the essential elements critical for studies that can firmly link chemosensory navigation to the fluid regime. This information is currently embodied in a number of fields of inquiry, and collecting it into a single place may help to define a set of approaches and tools to aid others in investigating orientation to chemical cues. Secondly, in reviewing studies on navigation, general patterns emerged that link certain sensory strategies to particular fluid environments. These connections are explored. In this regard, a particular problem is how to compare animals of widely differing size and scale. Proceeding from the discussion of fluid properties and animal strategies, I offer a basic model that uses nondimensional parameters to establish the dynamic similarity between animals in different flow environments. In much the same way as simple fluid dynamical quantities allow comparison of flow that is size and scale independent, developing methods for the non-dimensionalization of navigation may be a way for comparing abilities and locomotory performance in seemingly disparate creatures.

### Scope

I take as a model the problem of an animal finding a relatively discrete object, such as a food item or mate. This process is at an intermediate scale between processes that affect the microdistribution of odor signals around and through olfactory appendages (Kochl, 1996), and the large-scale mixing that determines the signals that wide-ranging animals use to find a source (Dittman and Quinn, 1996). The focus is on aquatic creatures, for two reasons. First, at biological scales of interest, fluid dynamics in air is somewhat intransigent; it has been difficult to quantitatively describe odor source dynamics in sufficient detail. Secondly, working in aquatic habitats affords an unparalleled opportunity to examine a large range of fluid dynamic environments. Orientation to olfactory signals has been shown to take place in viscous and turbulent flows that conservatively span a range of Reynolds numbers (see below) of at least 4 orders of magnitude (Weissburg, 1997). Considering orientation in diffusive environments or creeping flows experienced by microorganisms extends the lower boundary of the Re range by 100- to 1000-fold. At this stage of investigation, I believe it is comparisons across a large range of fluid mechanical states that will provide us the most insights into the coupling between navigational performance, sensory strategies, and odor properties. Although the experimental focus is predominantly in the aquatic realm, the results also may be relevant to terrestrial organisms. Analysis of flow rates, length scales, and fluid properties between air and water, and the organisms therein, suggests that they are dynamically similar environments with respect to odor signals entrained in flows. Similar behaviors expressed by various aquatic and terrestrial crea-

tures points toward convergent solutions to common problems of orientation and navigation in seemingly disparate odor landscapes.

### Mechanisms of Transport in Fluids

Broadly speaking, the movement of substances dissolved in fluids results from either one of two processes; diffusion, which represents the random molecular motion of substances, and transport by the moving fluid.

#### *Diffusion*

When fluid motion has a minor impact on the distribution of odorants, the chemical signal environment is accurately modeled by a well-known family of diffusion equations, as covered for instance, in Dusenbery (1992). The dynamics of a signal in this environment cause a rapid spread of the odorant front, which is symmetric from the point of origin, creating an exponentially decaying continuous gradient in the intensity of the chemical signal. The rapid initial spread of the odor cloud is followed by a slow decline through time that results in an increasingly shallower spatial gradient (e.g., Dusenbery, 1992). Since organisms have a defined threshold concentration for the induction of chemically mediated search, this results in a signal that reaches a maximum radius of detectability when the edge of the odor front is at the organism's perceptual limit. Thereafter, continued diffusion dilutes the odor concentration such that the active space that can be perceived by an individual diminishes, and the edge of detectability shrinks.

#### *Transport in flow*

When fluid motion cannot be ignored, the dynamics of odorant transport become considerably more complex. The concentration of odorants will reflect advection of the odorant by the mean (or bulk) flow, and diffusion due to turbulence. The general theory of turbulence is quite extensive and beyond the scope of this presentation, but it is essential to appreciate a few points. First, although turbulence is ubiquitous, it is not always an important aspect of fluid flow, and a number of flow environments in which chemosensory orientation takes place are largely free from this type of fluid motion. Second, turbulence is intrinsically a chaotic process in which local vectors and velocities of fluid motion vary unpredictably. Conceptually, flow streamlines in laminar flows remain parallel to each other, and therefore largely aligned with the direction of mean transport. In contrast, turbulent flows contain regions where local flows are oriented in any direction with respect to the bulk flow. Lastly, although turbulence may be quantified, only the intrinsic tendencies of turbulent fluid motion may be described by time-averaged descriptions of its intensity, spatial or temporal distributions, etc. Thus, unlike other flow

scenarios, it is impossible to predict the instantaneous odor concentration at a given point when turbulent motion is present. This simple fact has set serious constraints on our understanding of the properties of these signals and the animal strategies that are designed to operate in these environments.

In the ocean, turbulence arises from a variety of sources that operate on scales larger than that relevant for organisms tracking their predators, prey, or mates (Svendsen, 1997). These eddies tend to approximate the scale of the flow, and they correspond to a length on the order of the water depth or boundary layer thickness (see below, Sanford, 1997). However, the energy contained at large scales is transferred to successively smaller scales by a process known as the Kolmogorov cascade (Tennekes and Lumely, 1972). If we imagine that turbulent fluid motion is in the form of coherent eddy structures (those where flows are rotational), this process can be envisioned as the breakup of larger eddies into a series of ever smaller structures. This process reaches its lower limit when viscous interactions between fluid molecules dissipate the energy contained in fluid motion. This limit, the smallest eddy size containing turbulent energy, is the Kolmogorov length scale and is predictable from a variety of fluid mechanical quantities. Most importantly, increases in turbulence extend the energy cascade to smaller and smaller spatial scales before viscosity takes hold. In the open ocean, this lower limit is typically between 0.2 and 3 mm (Denman and Gargett, 1995; Jiménez, 1997; Sanford, 1997). An important consequence of the energy cascade is that regardless of the source of turbulence, at length scales in the millimeter range, the statistical properties ought to be independent of the mechanism and relate only to turbulence intensity (Jiménez, 1997).

Another important source of turbulence occurs where a fluid flows over a solid object. The fluid in contact with a solid interface is at rest and represents a momentum sink. Viscosity acts to dissipate momentum in the fluid so that turbulent structures appear, resulting in a cascade as described above (Schlichting, 1987). Even when fluid motion is initially laminar, this process will eventually result in boundary layer flows assuming a turbulent character. These flows are of great importance to many aquatic organisms that forage, escape, and seek dwellings on the sea floor.

### Useful Hydrodynamic Properties

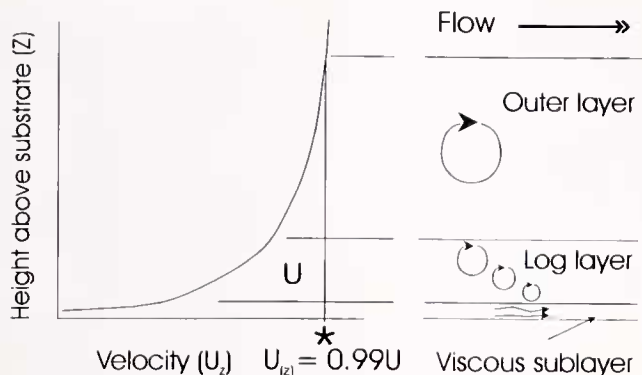
While the character of a flow is difficult to describe exactly, a number of useful parameters exist that allow a rough description of the nature of the fluid environment. These consist of a handful of dimensionless parameters that index the importance of various fluid properties or transport mechanisms. The most basic measure, which remains the starting point for discussions of fluid flow, is the Reynolds number:

$$Re = \frac{lU}{\nu} \quad (1)$$

where  $l$  is a length factor,  $U$  is fluid velocity, and  $\nu$  is kinematic viscosity. The Reynolds number represents the ratio of inertial to viscous interactions in the fluid, or alternatively, a ratio of the time scales of inertial transport *via* eddies to dissipation of momentum *via* molecular interactions in the fluid. When  $Re \ll 1$ , viscosity dominates, and the character of the flow is orderly and predictable. Particles move along streamlines that remain parallel to each other, a characteristic referred to as laminar flow. This is the regime most conducive to the modeling of chemical signal structure, since the relative unimportance of inertial forces largely restricts spreading of molecules to molecular diffusion. As  $Re$  increases ( $\gg 1$ ), inertia becomes the dominant force and the flow becomes increasingly chaotic. Local fluid velocity exhibits substantial fluctuations and is thought of as consisting of a variable flow component superimposed onto a mean flow. Turbulence intensity ( $u'$ ) then corresponds to the root mean square of velocity fluctuations. Unfortunately, no set point clearly demarcates the transition between laminar and turbulent flow regimes, and so  $Re$  is only a rough approximation that is best confirmed by measurement or visualization. The importance of turbulence for chemical signal transmission cannot be overstated. Even at moderate turbulence levels, such as those characterizing open-ocean environments (Gargett, 1997; Sanford, 1997), the rate of dispersion of chemical signals is by orders of magnitude greater than that sustainable by diffusive mechanisms.

Flows over solid objects are characterized by a distinct velocity gradient dictated by the no-slip condition at the object surface (Fig. 1). Fluid velocity is zero at the interface and increases logarithmically with height above the surface. This region of growth is termed the boundary layer and is taken to extend to the point where fluid velocity is 99% of the nominal (free-stream) value. The boundary layer grows as it moves over an object, and for a flat plate, the rate of increase is proportional to the square root of the distance from the upstream edge of the plate (Schlichting, 1987; Denny, 1988). At any given location, the thickness is inversely proportional to  $U^{1/2}$ . The dependence of boundary layer thickness on both distance and  $U$  presents difficulties for experiments conducted in flow channels, since the boundary layer thickness changes rapidly during its initial development. Flumes used to examine orientation behavior must present walking or crawling animals with boundary layers that do not change substantially during locomotion to the source (*e.g.*, Weissburg and Zimmer-Faust, 1993, 1994).

As for any flow, boundary layers may be laminar or turbulent, and the transitional  $Re$  can be evaluated in any number of ways. Over a smooth flat plate,  $Re$  must exceed  $3.5 \times 10^5$  to  $10^6$ , which corresponds to a water current of 0.34 to  $1 \text{ m s}^{-1}$ , for turbulence to result (Denny, 1993). In



**Figure 1.** Dependency of flow velocity  $U(z)$  on height above the substrate ( $z$ ) and structure within a turbulent benthic boundary layer. The boundary layer is defined as extending to the height where  $U(z)$  reaches 99% of the free-stream velocity, marked on the  $x$ -axis. The flow profile of a turbulent boundary layer profile is qualitatively depicted on the right, which shows the generation of large eddies in the outer layer, momentum transfer and the Kolmogorov cascade in the log layer (which accounts for approximately 30% of the total boundary layer), and laminar flow in the viscous sublayer. Note that whereas this example shows the boundary layer developing over a substrate, a turbulent boundary layer can develop over any surface immersed in flow.

this instance, the length factor,  $l$ , is the distance from the leading edge, and the resulting quantity is often referred to as the local  $Re$ . A more precise relationship given by Pedley (1997) specifies that the  $Re$  must exceed 244 when  $l$  is the boundary layer thickness. It is evident from these relationships that many, if not most, boundary layer flows of biological interest will be turbulent, particularly when chemical signals are entrained in flows over a substrate. Also, note that the intensity of turbulence is not constant in these types of flows;  $u'$  is maximal in the region of the boundary layer where the relationship between velocity and the log of the height above the substrate is linear (the log-layer). In open channel (e.g., flume) flows,  $u'$  seems to reach a peak where  $Z/H \approx 0.05$ , where  $H$  is the flow depth (Nezu and Rodi, 1986) and  $Z$  is height above the substrate. It is therefore likely that many animals will have sensors in locations within the boundary layer where turbulence is rather vigorous.

Like politics, boundary layers are local phenomena. The practical choice of length and velocity scales is contingent on the precise relationship between the object of interest and the flow in its immediate vicinity. Whereas the benthic boundary layer is the signal environment for a foraging crustacean, a parasitic copepod investigating the olfactory cues on a moving blue crab is more strongly affected by the boundary layer around its target than by the flow over the substrate. Multiple boundary layers exist simultaneously, and the choice of inappropriate parameters will result in a poor characterization of the relevant flow properties.

The character of boundary layer flows is often related to the roughness Reynolds number,

$$Re^* = \frac{u^*D}{\nu} \tag{2}$$

where  $u^*$ , is the shear velocity and  $D$  is the hydraulic roughness length, which for nonrippled substrates corresponds simply to the diameter of the grains forming the bed (e.g., Weissburg and Zimmer-Faust, 1993). The shear velocity is the scalar of momentum flux in a boundary layer, or roughly, the velocity at which momentum is transferred. It thus is an index of the extent to which turbulent (shear) stresses are transmitted through the boundary layer. A number of authors provide rules of thumb or empirical relationships for estimating these quantities (e.g., Denny, 1988). Observations suggest that the outer regions of a boundary layer begin to feel the effects of turbulence when  $3.5 < Re^* < 6$ , and the turbulence extends all the way to the bottom when  $75 > Re^* > 100$  (Schlichting, 1987).

As previously discussed for the open ocean, turbulent fluid motion in a boundary layer is involved in a cascade that transfers fluid mechanical energy to smaller and smaller spatial scales. Again the largest eddies approximate the scale of the flow, and the lower (Kolmogorov) limit,  $\eta$ , is related to turbulence intensity (Tennekes and Lumley, 1972):

$$\eta = \left[ \frac{kZv^3}{u'^3} \right]^{1/4} \tag{3}$$

where  $k$  is the empirically derived von Karman's constant equal to about 0.4. However, molecular diffusive forces continue to redistribute chemical signals (and other scalar quantities such as heat), so that the length scale of the smallest scale fluctuations of these quantities ultimately is determined by the molecular diffusivity  $D_m$ :

$$\eta_s = \left[ \frac{\eta v}{D_m} \right]^{-1/2} \tag{4}$$

where  $\eta_s$ , the Batchelor microscale, is smallest size for chemical fluctuations (Mann and Lazier, 1991). In open-ocean conditions, this limit is estimated to be on the order of  $10^{-2}$ – $10^{-4}$  m (Sanford, 1997), while it has been empirically measured to be  $10^{-4}$  m or smaller in benthic boundary layer flows at moderate shear velocities (Moore *et al.*, 1992).

Although  $Re$  can provide some estimate of the importance of inertial vs. diffusive transport, its utility largely stems from its relationship to turbulence. In an attempt to further clarify the role of flow vs. diffusion in biological situations, a number of workers (e.g., Moore *et al.*, 1999) have used the Peclet number:

$$Pe = \frac{lU}{D_m} \tag{5}$$

This quantity is a more direct index of the importance of advective transport relative to molecular diffusion. Since

the time scale of diffusion is proportional to  $l^2/D_m$ , and the time scale of advection to  $l/U$ , the Peclet number also is accurately viewed as an index of diffusive to advective time scales. As Pe increases, diffusive processes are relatively less important in governing the rate of delivery of a chemical species to an organism or its sensor. Pe is far greater than unity in most contexts, such as a lobster moving through a turbulent odor plume. The distance ( $l$ ) over which chemical cues must be transported is large, and advection is the predominant mechanism. In contrast, molecular diffusion assumes an important role in the movement of materials around microorganisms or individual sensilla. In these cases the length scales are small, and fluid velocity is often low since the structure may lie within a boundary layer.

A parameter that has so far received far less attention by workers investigating odor signal transmission is the Strouhal number. This parameter relates to the frequency with which eddies are generated by an object in flow. For a cylindrical object, such as a bivalve siphon that projects with its long axis into the flow, vortices are shed alternately from the top and bottom with a predictable frequency,

$$St = \frac{fD}{U} \quad (6)$$

where  $D$  is the diameter, and  $f$  is the frequency of vortex shedding. Interestingly,  $St$  is roughly constant when  $100 > Re > 10^5$ , meaning that for an object of a given diameter, there will be a linear increase in shedding frequency with velocity (White, 1991). Over most of this range, the regularly alternating pattern of shedding, known as a vortex street, is present. A vortex street may exist at an  $Re$  of up to  $10^7$ , although it becomes increasingly chaotic (Lugt, 1995). Such vortices can presumably entrain odorants and impose a dominant frequency on signals transmitted in their wake, although there has been little experimental work on this aspect of fluid flow.

### Biologically Relevant Signals

#### *Signals in the diffusive realm*

Chemical signals in which diffusion is the predominant transport agent include gradients followed by bacteria and other small organisms. These types of situations are particularly amenable to modeling, given the ease with which diffusional gradients may be represented analytically with a small number of physical constants. Key observations are that locating a source in these environments is affected by properties such as animal size, shape, motility, and gradient strength (Dusenbery, 1997, 1998a, b). The mechanism most frequently identified is indirect orientation (kinesis *sensu* Dusenbery, 1992), in which travel in the direction of increasing stimulus strength results in a decreased probability of changing direction (Berg, 1975). In general, a gradient

may be sampled using either spatial or temporal comparisons. Larger animals are at an advantage, since they can spread receptors over a greater distance and move more rapidly, thus increasing the ability to sample gradients in either the temporal or spatial domain. Additionally, for the smallest unicells, Brownian motion will set constraints on sampling by rotating the cell and changing the orientation of receptors on its surface. As a result, although spatial sampling is generally superior, temporal sampling is favored in weak gradients and low stimulus concentrations that require longer stimulus integration times (Dusenbery, 1998a). Although there are few systematic comparisons, temporal sampling is the commonly observed strategy, perhaps because it extends the range of gradients that contain useful information. Since it is possible to solve for the critical gradient decay lengths that determine the effectiveness of each type of sampling mechanism, it may be possible to arrive at general conclusions about the environments and organisms in which each type of mechanism should be found.

Organisms that respond to chemical cues in diffusive environments are not only bacteria, but also ciliates (Verity, 1988), flagellates (Crenshaw, 1996), and spermatazoa of both plant and animals (Ward *et al.*, 1985). One common thread among these representatives of diverse phyla is that they often move along a helical trajectory. Helical motion occurs when a body rotates around its central axis and translates through space simultaneously. Crenshaw, in a series of papers (reviewed in Crenshaw, 1996), has refined the mathematical and observational tools necessary to quantitatively analyze this type of behavior. He finds that by suitable adjustments in the rotational velocity, animals or cells can align the axis of their helical path along a chemical gradient, providing another mechanism for orienting to chemical gradients that is successful over a wide range of kinematic parameters (Crenshaw, 1993). This mode of orientation is suitable for an organism that has a single chemoreceptor on its surface, or a population of receptors distributed equally across its body, and that depends on temporal comparisons of stimulus intensity obtained as it moves through the gradient. This mode of orientation is thus a special class of klinotaxis (temporal sampling), designated as helical klinotaxis by Crenshaw (1996), and represents a direct guidance mechanism. To date, this strategy has been identified only in cells or organisms propelled by flagellar or ciliary motion in very low  $Re$  environments. In these situations, where flows are reversible, propulsion is achieved only by asymmetric motions of the cilia or flagella, and this may create movement that is naturally helical.

Diffusive transport is also common for larger creatures tracking both food (Hamner and Hamner, 1977) and mates (Weissburg *et al.*, 1998; Yen *et al.*, 1998). Males of the copepod species *Temora longicornis* can track females over trail lengths as long as 10 cm, or about 100 body lengths

(Doall *et al.*, 1998; Weissburg *et al.*, 1998; Yen *et al.*, 1998). Calculated on the basis of the average size (1–2 mm) and swimming velocity (3–6 mm/s) of these copepods, the  $Re$  of these flows is about 0.3–0.6. Here, the slow diffusive transport of chemical signals compared to the relatively rapid diffusion of momentum creates (see Yen, 2000) a chemical signal that more properly resembles a coherent trail hanging in three-dimensional space. There is no flow information present, and behavioral analysis strongly suggests that spatial comparisons facilitate detection of the diffusing trail edges, whereas temporal comparisons mediate up-gradient progress (Weissburg *et al.*, 1998). It is important to note that, in this case, diffusion acts not as an agent of transmission but in precisely the opposite manner; slow diffusion restricts the spread of chemical signals, thus favoring the existence of a defined chemical trail. The edges of the trail move only a few hundred micrometers during the trail's useful life, and the difference in concentration along the length of the trail is estimated to be only 100-fold. Early reports (Katona, 1973) argued for diffusion as a transport mechanism bringing the pheromonal cue to the expectant male, but the time scales over which this operates are clearly too long to account for observed behavior (Yen *et al.*, 1998).

Orientation in these low  $Re$  situations appears to be a fundamentally different set of mechanisms than those postulated for orientation in turbulent flows (see below), particularly because there is little flow information to aid the animal in determining the up-gradient direction. Flow information may be restricted to situations in which animals shed more intense fluid disturbances, as when some plankters transiently achieve velocities of several hundred body lengths per second (Yen and Strickler, 1996), and reach a fluid regime that is transitional between laminar and turbulent flow. Vortices are shed during this transition that also appear to be used in mate tracking in the copepod *Acartia hudsonica* (Doall *et al.*, 1999). Perhaps animals detect chemical signals in these structures as well, and use these flavored eddies to locate their mates by relying on both flow and chemical signals. Some animals that seem to rely on chemical trails do so in conjunction with other cues that supplement the information obtained from perception of odor. The swimming patterns of a number of copepods and other plankton such as shrimp and bivalve larvae suggest that the perception of a chemical cue invokes downward movement (Hamner and Hamner, 1977; Tamburri *et al.*, 1992; Tsuda and Miller, 1998). For animals that track sinking or downward-swimming objects, use of gravity is a quite reliable strategy for resolving ambiguity about the direction in which the trail was made. Odor becomes a stimulus that releases geotactic orientation behavior, which frees the animal from having to perform complex processing to extract gradient information from the chemical signal itself.

For animals that operate in these low  $Re$  environments,

diffusive transport preserves trail coherence. Ambient fluid motion and turbulent mixing may dissipate or break a trail, resulting in a signal that cannot easily be tracked, particularly through the use of odor alone. As suggested above, one compensatory strategy is to use supplemental cues that are correlated with general direction towards the source. Another is to perform olfactory guided behaviors in environments where dissipative forces are minimal. Some species of copepods appear to aggregate where the rate of energy dissipation is low (*e.g.*, Mackas *et al.*, 1993; Inceze *et al.*, 1996), perhaps because stable zones in the ocean are the most permissive of navigation along diffusive trails and extend the spatial and temporal limits over which these trails can guide animal movement. It is unknown whether animals in the field commonly follow trails over distances as long as those observed in the laboratory.

### Signals in turbulent flows

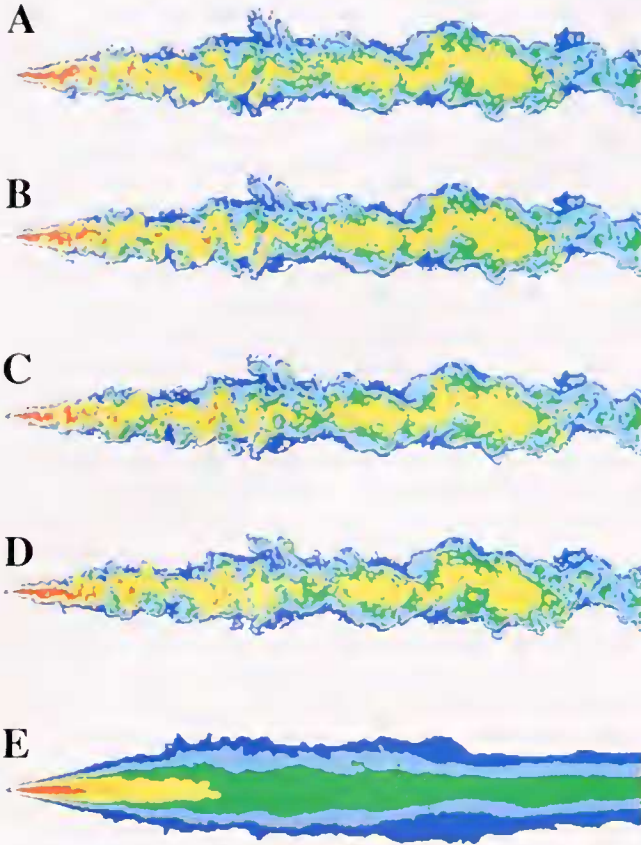
Given the magnitude of fluid motion (centimeters per second to meters per second) and length scales (centimeters to meters) in which creatures such as insects, decapod crustaceans, fish, echinoderms, and gastropods operate, many will track objects in regimes where turbulence is a prevailing aspect of the flow. Studies of moths over several decades have led to an acute appreciation of the consequences of this fact and forced us to revise many of our ideas on chemosensory tracking. The most critical change in thinking has been an abandonment of diffusion models of odor plume structure as a way to examine stimulus concentration.

The earliest formulation of time-averaged plume structure applied to insect navigation was derived by Sutton (1953); it solves for the concentration  $C$  from a source emitting continuously at a rate  $J$ , for a point at a downstream distance  $r$  and angle  $\theta$  from the midline of the plume:

$$C_{(r,\theta)} = \frac{J}{4\pi r D_e} \exp\left[-(1 - \cos \theta) \frac{rU}{2D_e}\right] \quad (7)$$

Here,  $D_e$  is a constant of eddy diffusivity, a measure of dispersion by turbulence that is analogous to the molecular diffusivity and which must be empirically determined depending on the flow scenario. The odor concentration is Gaussian across the axis of the plume, but it decays with  $1/r$  in the downstream direction. Other formulations are specific to particular types of flows, such as the equation derived by Pasquill and Smith (1983) for boundary layers. An advantage of this model is that it uses  $u^*$ , an easily derived quantity.

Whereas the equations give the time-averaged structure of the plume (Fig. 2), the animal itself uses chemosensors that operate at fine spatial and rapid temporal scales and perceives the plume as a series of filaments of intense odorant concentration interspersed with periods when the



**Figure 2.** Instantaneous vs. time-averaged views of odor jets. This picture is a series of laser-induced fluorescence (LIF) images of dye concentration of an odor plume in flow (concentration expressed as color: red is highest, blue is lowest concentration). A–D represent a series of images on a rapid time scale (4 ns frame, 30 ns between successive frames), and show the fine-scale structure of the plume. Note how coherent eddy structures persist and move downstream. E is an average of about 1000 images, and is equivalent to modeling the time-averaged structure of the plume using equation 7. The jet is approximately 1 m long and 15 cm wide, with an initial source concentration of rhodamine 6G equal to  $200\mu\text{g/l}$ .

concentration is low or undetectable. Given the nature of turbulence, there is appreciable variation in the intensity and duration of each odor filament, and the information represented by turbulent diffusion models does not depict the signals received by the animal. It has been known for some time (reviewed by Murlis *et al.*, 1992; Vickers, 2000) that insects do not respond to mean concentrations predicted by these models. A recent report concerning aquatic plumes suggests that a tracker averaging a finite series of instantaneous measurements of odor concentration cannot estimate the time-averaged Gaussian plume structure (Finelli *et al.*, 1999) during navigation. Extracting information from each contact with a discrete odor pulse is the only alternative.

The filamentous structure of odor plumes has been reasonably well characterized in marine realms, at least under certain conditions. Investigators using flow visualization

techniques, as well as chemical microprobes that measure at fine spatial and temporal scales, have verified that aquatic odor plumes consist of rapidly fluctuating signals (Moore and Atema, 1991; Moore *et al.*, 1994; Finelli *et al.*, 1999). Patchy odor distributions are a general rule for conditions under which animal tracking has been observed in the laboratory. At turbulence levels characteristic of natural habitats ( $u^* \approx 0.1-1$ ), odor pulses generally are brief ( $<1$  s) with long periods of odor absence. Consistent with studies in terrestrial habitats (Murlis *et al.*, 1992), intermittence reflects two processes with different spatial and temporal scales. The largest scale eddies cause the plume to meander across stream, imparting large periodicity to the fluctuations of odor intensity at a single point. This process continues until the plume is dispersed to about the same size as the large flow structures. Concomitantly, the plume remains relatively coherent on a small scale until its width exceeds the Kolmogorov size. Thereafter, it becomes torn apart and filamentous due to the action of turbulence at these scales.

Aquatic animals tracking waterborne odor plumes display movement patterns that are consistent with the general mechanisms proposed for insects (Vickers, 2000). When tracking odor plumes, various animals use zig-zag trajectories, including decapod crustaceans (Moore *et al.*, 1991; Weissburg and Zimmer-Faust, 1993), salmon and sharks (Johnsen, 1987), and deep water macrourid fish (Tamburri and Barry, 1999). These behaviors are either the result of an internally generated pattern of counterturns released by odor contact, as has been postulated for salmon and sharks (Johnsen, 1987), or are the result of movements to opposite edges of the plume, coupled with a subsequent turn into the main axis that is mediated directly by the stimulus itself (Weissburg and Zimmer-Faust, 1993, 1994). In lobsters, evidence gleaned from simultaneous recording of stimulus patterns and animal movements strongly suggests that differences in odor concentration across the body axis turn the animal towards the stronger stimulus and back into the plume (Atema, 1996). Blue crabs seem to track along the edges of odor plumes quite well in the field, lending further support to this perceptual mechanism. This tropotactic discrimination of boundaries is the same strategy as that postulated for tracking copepods, and depends on reasonably discrete plume edges that permit the detection of stimulus asymmetry. As the plume widens, zigzagging is expected to be more pronounced, and observations of blue crab behavior in turbulent flows show this to be the case (Weissburg and Zimmer-Faust, 1993, 1994). Again, the parallels between animals in high vs. low Re flows are striking; male copepods also increase their tacks across the trail when females lay down more diffuse signals (Weissburg *et al.*, 1998).

One of the consistent elements in the tracking of aquatic chemical trails is the reliance on flow as an orienting stimulus released by the detection of odor. Blue crabs (Weiss-

burg and Zimmer-Faust, 1993, 1994), sharks (Hodgson and Mathewson, 1971), and a number of species of fish (Johnsen, 1987), flatworms (Bell and Tobin, 1982), and gastropods (Brown and Rittschof, 1984) all show odor-conditioned response to flow or have difficulty locating odor sources in quiescent environments. Odor-conditioned rheotaxis may be the aquatic analog of amenotactic responses displayed by insects.

One of the major difficulties in studying orientation in turbulent flows is that the odor and flow information available to the animal is impossible to either compute or model with the required degree of complexity. One approach is a throwback to the early days when investigators applied Suttonian diffusion models to plume dynamics. Thus, Baird and his colleagues (Jumper and Baird, 1991; Baird *et al.*, 1996) have applied turbulent diffusion approximations to compute the spread of pheromones from midwater fish. Using empirically determined coefficients of turbulent diffusion, they model the concentration gradient of an odor cloud as it changes through time. Turbulent diffusion constants are analogous to molecular diffusion constants but are  $10^5$  to  $10^6$  times greater, since transport occurs by turbulent flow instead of random molecular motion. These types of models have the advantage of calculating odor gradients using measured physical constants, and they capitalize on the fact that midwater habitats are unbounded and thus amenable to modeling using a simple diffusion approximation. These models have produced useful conclusions about the time and space scales over which these clouds remain detectable, but one potential problem is that they do not consider the fine-scale structure that may be so critical in orientation. However, animals in these situations might indeed track gradients by having stimulus integration times that exceed the relevant scales of the fine structure imbedded in the odor cloud. Only recently have we had sampling capabilities at spatial scales (centimeters to meters) that would allow us to answer the question of whether a swimming fish is more likely to perceive such structures as gradients or as a series of discrete patches. If the former, then studies of bacterial chemotaxis become more relevant because they have identified a number of key parameters that affect orientation efficiency. Animal size, movement speed, and tendency to be randomly reoriented during search should prove to be as critical for orientation in gradients produced by turbulent diffusion as they are for those produced by molecular diffusion.

### Behavioral Implications of Fluid Flow Regimes

#### *High vs. low Re environments*

Although the important elements of the various flow scenarios cannot be easily summarized, a crude but accurate perception is that low Re viscous environments are characterized by slowly changing signals, low flow, and continu-

ous gradients. In contrast, high Re regimes produce a signal structure that is chaotic, intermittent, and occurs against a bulk flow that is perceptible to navigating animals.

A consequence of these dramatic differences is that animals inhabiting various fluid milieus may have arrived at different orientation strategies. Animals in turbulent environments are likely to rely on flow to provide a general direction towards the source, since extracting this information from the odor signal itself appears challenging. Animals in these environments also utilize flow to narrow their search windows in the absence of odor, and cast across stream when they initially search for, or lose contact with, the plume (Weissburg and Zimmer-Faust, 1993, 1994).

A copepod searches for its mate in a viscous realm, where the Re is roughly  $10^3$  to  $10^4$  less than that of a typical decapod, and consequently relies on mechanisms other than those used by their larger brethren. Without flow, copepods search in three dimensions to locate the odor boundaries, and direction towards the source comes only from temporal comparisons of odor intensity (Doall *et al.*, 1998; Weissburg *et al.*, 1998; Yen *et al.*, 1998). Interestingly, animals in both types of environments seem to use similar methods of edge detection, suggesting that for both diffusive trails and turbulent plumes, the borders of a signal source retain sufficient integrity and gradient steepness to be perceptible by spatial sampling.

A second fundamental difference between animals in diffusive vs. turbulent regimes may be the integration time over which they acquire chemosensory information. For animals in turbulent flows, the transient nature of the stimulus forces the sensory system to rely on rapid integration of brief odor pulses. Lobster olfactory neurons can encode some stimulus features in about 200 ms (Gomez and Atema, 1996), which is clearly an adaptation to a filamentous plume structure. Although the time constants of other aquatic organisms are not known, a reasonable expectation is that animals that follow gradients may have slower integration times.

One of the greatest challenges in research on chemosensory orientation in high Re environments is to understand how animals extract information from the evanescent signals that characterize turbulent flows. Although tropotaxis seems a robust mechanism for edge detection, the strategy mediating movement to the source is less well known. In principle, odor pulses in aquatic odor plumes may contain information that can be used to extract directional information (Atema, 1996), and investigators have proposed that some animals may use this information during tracking (reviewed in Weissburg, 1997). However, this type of strategy seems considerably more complex than a simple mechanism whereby the mere detection of odor presence triggers a response to an orienting stimulus (flow, gravity, light) that points to the source.

The above arguments suggest that further studies of che-



mosensory navigation should consider the potential interactions between chemical cues and other stimuli. For animals that perceive current, perhaps navigation in response to the detection of individual, rapid odor transients is restricted to a range of narrow conditions comprising relatively swift unidirectional flows. Sadly, there is little information on perceptual limits in response to flow. Ebina and Wiese (1984) suggest that crayfish align to current velocities as low as 0.1 cm/s, but comparative data are lacking. The consequences of oscillatory flows, or complicated flow patterns that occur in the presence of underwater structural heterogeneity, are also unknown. Do animals in these situations extract information from properties of odor pulses, or do they have other strategies? Lastly, studying animals with a fixed frame of reference may bias our perspective. In their three-dimensional world, fish or other midwater animals may not have access to other orienting stimuli unless the odor is predictably aligned to the vertical axis. Current direction would generally not be perceptible to the fish from its own Lagrangian perspective, except in certain unusual cases. Westerberg (1984) presents an interesting hypothesis describing the use of shear gradients at strong density discontinuities to detect flow direction. It is unknown whether such animals have a means of detecting flow, extract information from properties of odor pulses, or follow gradients. If the last alternative is true, then turbulent diffusion models capture the necessary signal properties. Of course, gradient-following mechanisms set serious limits on orientation, since the integrated signal (which will be weaker than the peak intensities in a pulse) must be perceptible, and intensity differences must be detectable through space or time.

#### *Nondimensional parameterization of behavior*

Now that we have a number of animal models for orientation in flows, it becomes possible to take a comparative approach. Simply put, is the behavior of a blue crab (or lobster) functionally the same as that of a moth? The directness of the question disguises the complexity of the answer, since the resolution requires us to compare animals of different sizes, movement velocities, and taxonomic affiliations that live in differing fluid regimes.

One of the strengths of hydrodynamic theory is that the character of the flow can be compared across habitats and in different fluids by using  $Re$ ,  $Pe$ , etc. However, this is only a partial solution, and a more definitive answer requires us to compare the behavior of animals with respect to the properties of the flow, rather than simply comparing the flows themselves. In effect, we must arrive at nondimensional quantities for behavior in relation to fluid flow. Proceeding from the idea that a few simple quantities may help identify such a comparative framework, I present two such nondimensional parameters that incorporate hydrodynamic and behavioral properties. Clearly, this is a first attempt, and its

real utility may be to suggest approaches of greater rigor that incorporate more realistic assumptions and quantities.

Consider an animal in flow that has a fixed frame of reference as it moves in an odor plume (Fig. 3). The animal moves at a constant velocity  $v$ , and samples its environment with a fixed frequency  $f$ . Its navigational strategy encompasses two critical tasks: it must move in the direction of increasing stimulus intensity, and it must stay within the borders of the plume.

The results of our previous studies of insects and crustaceans suggest that the key parameter mediating up-gradient progress is the rate of contact with discrete odor filaments. These studies also emphasize the importance of rapid sampling, since individual measurements collected over a longer time period result in dilution by mixing odor-containing filaments with clean fluid. This may render average concentrations below the limits of detectability. Animals can, however, gain information about the properties of the plume at a given location by collecting a number of rapid samples and then averaging these measurements. Successive averaging of odor pulse properties (intensity, slope, length, etc.) could then be used to judge progress towards the source. In essence, this is the method used by various investigators to reconstruct the time-averaged properties of a plume along its length and breadth, using a sensor that collects a number of rapid samples at a series of discrete locations.



**Figure 3.** Illustration of the parameters used to calculate the temporal and spatial integration factors (TIF and SIF respectively). A lobster with an antennular span  $A$  and sampling frequency  $f$ , is moving at velocity  $v$  in an odor plume with a Kolmogorov size  $\eta$ . The overall width of the plume is given by the characteristic eddy size  $L$ .

The mechanism described above depends on the animal's sampling rate relative to the scale of variation in the odor plume. Assume that the Kolmogorov limit represents the length scale of the fine structure of the plume. Then, it becomes possible to define the temporal integration factor (TIF), a nondimensional estimate of the sampling ability of the animal, as:

$$\frac{\eta}{\sqrt{f^{-1}}} \quad (8)$$

When this number exceeds 1, the animal is either sufficiently slow or samples with sufficient rapidity to detect many odor filaments at each point in the plume that it moves through. In other words, as TIF increases, the animal increases its ability to reconstruct the time-averaged view of the odor through an average of a number of instantaneous samples. A  $TIF \ll 1$  corresponds to extremely intermittent sensing of the plume.

A similar number may be defined for integrating across space, and I assume that the ability of an animal to determine its position transverse to the plume axis corresponds to the spatial integration factor (SIF). The SIF represents the width of the animal's sensor span (its ambit,  $A$ ) relative to the width of the plume, which as a first approximation is on the order of the length scale of the dominant eddy size  $L$ . Thus, the SIF is:

$$A/L \quad (9)$$

When SIF is large, the animal samples broadly across the plume and has a high probability of detecting an edge beneficial for tropotactic orientation. When SIF is small, the animal is less able to determine its position from information obtained at a single location, and is therefore more likely to move across stream during navigation.

I calculated TIF and SIF for aquatic and terrestrial arthropods, using published values. Crabs and lobsters move at velocities of 1–10 cm/s (Moore *et al.*, 1991; Weissburg and Zimmer-Faust, 1994), and various species of moths fly through odor plumes at speeds of 30–100 cm/s (*e.g.*, Baker and Haynes, 1987; Mafra-Neto and Cardè, 1998). The Kolmogorov scale ranges from about 0.1 to 1 mm for aquatic benthic habitats, evaluated at a height of 6 cm above the bed (the approximate location of the antennules), using either published values (Sanford, 1997) or calculations based on measurements in laboratory flumes or field sites (Weissburg and Zimmer-Faust, 1993; Finelli *et al.*, 1999). Kolmogorov scales in terrestrial habitats range from 1 to 10 mm (Murlis *et al.*, 1992). Length scales,  $L$ , in crustacean habitats are expected to be on the order of 10 to 100 cm, based on typical flow depths in environments favored by blue crabs, and in terrestrial realms range between 1 and 10 m (Murlis *et al.*, 1992). Ambit sizes may be either the maximum body diameter, as for animals that use chemosensors across the

body surface, or the spread of olfactory appendages such as antennae. I used values ranging from 1 to 10 cm for crustaceans, and 1 to 10 mm for insects. Sampling rates for aquatic and terrestrial arthropods are assumed to be 4 and 10 Hz, respectively, based on an analysis of physiological properties of their chemosensory systems (Christensen *et al.*, 1995; Atema, 1996).

The TIF values for aquatic animals range from 0.4 to 0.004, and for moths calculations give values between 0.3 and 0.001. SIF values are about 1 to 100 and  $10^{-2}$  to  $10^{-4}$  for aquatic and terrestrial arthropods respectively. Both the smaller ambit and the larger length scales conspire to produce the very low SIF scores in moths as opposed to crustaceans. We may be underestimating  $L$  in marine habitats given the narrow range of natural flows that have been examined, and these SIF scores may decrease with further investigations.

The computations indicate that animals in both realms sample on a similar scale relative to the fine structure of the plume, although aquatic creatures have a larger ability to compare across the spatial domain. This latter observation may explain why crabs and lobsters seem to rely on tropotactic comparisons, whereas moths have no similar mechanism. In neither case do the TIF scores suggest much of an ability to acquire a time-averaged view of the plume on the basis of a series of rapid samples. This is in accordance with the bulk of current behavioral observations that animals use odor perception simply to release orientation to flow or wind direction. For both terrestrial and aquatic organisms, sampling rates must increase at least threefold for their abilities to match the pulse length scales in even the most benign conditions, and increases of 100- to 1000-fold are required to permit extensive sampling in most habitats. It may be impossible for chemosensory transduction to operate at sufficiently high frequencies to be generally useful as a means to acquire this type of time-averaged information, given that response latencies of olfactory cells range from 50 to 500 ms (Restrepo *et al.*, 1995). Decreases in locomotory velocity also may be untenable in light of the magnitude of the necessary reduction, particularly for flying animals that must maintain sufficient speed to remain airborne. Substrate-bound animals face no such constraints beyond the need to find distant objects within a limited time, but this still may prevent them from moving slowly enough to achieve the necessary sampling rates. Consequently, the pressures imposed by the scales of plume variation may have forced the evolution of sensory strategies that do not rely on the ability to time average. Interestingly, the TIF scores suggest dynamic similarity of navigational strategies, and moths and aquatic creatures may have converged on similar sampling capabilities relative to the fine-scale structure of their respective odor environments.

Moths and crabs occupy different quadrants of a  $2 \times 2$  matrix of TIF vs. SIF scores (Table 1). I am unable to

Table 1

*Temporal and spatial integration factor scores versus organismal and behavioral properties*

Spatial Integration Factor (SIF)	Temporal Integration Factor (TIF)	
	Low	High
Low	Low sampling rate and low spatial integration. Probable strategy: odor-conditioned taxis. Representative animal: moths.	High sampling rate and low spatial integration. Probable strategy: chemotaxis. Representative animal: gastropods?
High	Low sampling rate and high spatial integration. Probable strategy: odor-conditioned taxis and tropotaxis. Representative animal: lobsters, blue crabs.	High sampling rate and high spatial integration. Probable strategy: chemotaxis and tropotaxis. Representative animal: sea stars?

The table defines the four possible combinations of TIF and SIF that represent the different states of animal sampling with respect to their fluid dynamic environment, and describes, for each, the relative abilities to sample in spatial and temporal domains, the probable strategies that will result in effective orientation, and the types of organisms that might be expected to display these abilities. In these cases, chemotaxis refers to the use of temporal comparisons of gradient strength, and tropotaxis corresponds to spatial sampling.

uncover examples of animals that sample at a fine scale (high TIF), although in principle, such conditions are possible. In aquatic realms, slow-moving animals with sensors deep within the boundary layer may represent such cases, and they may operate in a milieu accurately modeled with time-averaged Gaussian formulations. Echinoderms are relatively large, but not fleet of foot, suggesting high scores for both SIF and TIF. Although sampling frequency for these animals is unknown, even very low values still allow sufficient resolution at the boundary layer conditions relevant to crustaceans; with a 10 mm/s movement speed (*e.g.*, Moore and Lepper, 1997) and a sensor height of 1 cm, a 1 Hz sampling frequency gives a TIF of 10. Gastropods are a likely candidate for possessing high TIF but low SIF, given their sluggish crawling speed and small size. On the basis of the foregoing analysis, we might expect an echinoderm to employ a combination of temporal and spatial sampling strategies, but spatial comparisons are unlikely to be of use to a gastropod.

The foregoing analysis does not imply that fine temporal sampling is impossible in air. In fact, it may be even more likely in air under appropriate conditions, since kinematic viscosity in air is 8–14 times greater than in seawater over a temperature range of 0°–30°C. Thus, under equal flow velocities and turbulence conditions, and for animals of equal size and movement velocity, the Kolmogorov size limit is about 4.75–7 times larger (eq. 3) in air than in water. Put another way, an insect could move seven times more quickly, or sample seven times more slowly, and have the same temporal sampling ability as an oceanic creature under similar flows. Indeed, the low TIF in insects is primarily a function of their exceedingly high flight speeds, suggesting that crawling or walking terrestrial arthropods potentially could act in a way similar to that of denizens of the aquatic benthos.

### Unresolved Issues

Our understanding of the mechanics of navigation, particularly in turbulent flows, is still in its infancy. Although a model incorporating rapid responses to odor filaments, tropotactic edge detection, and reliance on flow captures the essence of the orientation strategy, substantial gaps remain. Of immediate concern is identifying the range of critical stimulus parameter values that results in effective orientation. If up-current progress is largely mediated by the presence of detectable odor pulses, as it appears to be in moths (Vickers, 2000), then deleterious effects of turbulence may simply be due to increased intermittence that makes sustained progress less likely. During pheromonal tracking, the upstream surge of a moth in response to odor decays rapidly, and the moth begins to move cross-stream between successive stimulations. Rare encounters with odor pulses result in large cross-stream tracks that may take the insect out of contact with the plume, and that result in indirect trajectories to the source. Increased turbulence also causes more indirect trajectories in blue crabs (Weissburg and Zimmer-Faust, 1994), and this movement pattern seems to be correlated with greater signal variation and intermittence (although the expanded width of the odor plume and the inaccuracy of edge detection mechanisms may also be partially responsible). However, many foraging animals appear to respond to both the variance and the mean values of encounters with prey (Stephens and Krebs, 1986), and these two parameters interact to affect behavior. One possibility is that as the concentration of the odor pulse is increased, tracking occurs at more intermittent conditions as well. Such a scenario would hold if the propensity to engage in cross-stream casting in the absence of odor decreases with concentration, and it would be interesting to explore the potential interactions between intermittence and peak odor intensity during chemosensory tracking.

It is also clear that at this stage we have examined only a narrow range of stimulus conditions, and have rarely characterized the flow using standard fluid mechanical descriptors. One newly emerging issue is how the interaction between the release properties of the signal source and the ambient flow affects the resulting signal. Using laser-induced fluorescence to map odor concentrations at a fine scale, initial studies (Roberts, Webster, and Weissburg, unpub. obs.) suggest that the difference between jet and current velocities strongly determines the character of the signal (Fig. 4). When the jet velocity is matched to that of the ambient flow, plumes appear highly filamentous, and coherent structures retain their integrity far downstream of the source. As jet velocity is increased, the plumes become mixed more thoroughly, and the fine-scale features tend to vanish within a cloud of increasing homogeneity. These effects are most probably due to changes in shear-induced mixing at the border between the jet and the ambient fluid. As the velocity differential increases, the shear between the jet and the fluid is more pronounced, and results in greater mixing between the odor-laden jet and the clean water surrounding it. Previous studies have tended to use jets with high exit velocities relative to the ambient fluid (Weissburg, 1997; but see Finelli *et al.*, 1999), which nicely mimic certain types of odor sources (*e.g.*, actively pumping bivalves), but not others (*e.g.*, passively leaking objects). Before coming to firm conclusions about the nature of olfactory orientation, prudence dictates further exploration of the behavior of animals under different odor release conditions and geometries.

A real challenge for future investigators will be to verify that the plume morphology observed in flume flows adequately reflects plume structure in the field. The savvy student of chemosensory navigation in turbulent flows needs to be aware that laboratory characterizations have sometimes been compromised by inadequate flume designs. Acceptable principles of flume geometry and flow manipulation have been articulated, most recently by Nowell and Jumars (1987), and are summarized in Zimmer and Butman (2000). Unfortunately their recommendations have not always been incorporated into studies of animal navigation or chemical signal properties. Even when appropriate flow channels have been utilized, work in open-channel flumes incorporates strong assumptions regarding the properties of bottom boundary layers (*e.g.*, fully developed equilibrium flow) that may or may not be realized in the field. Studies in natural habitats are rare, and they have sometimes validated, at least qualitatively, the more extensive laboratory studies. However, in at least one case, boundary layers observed in nature are not consistent with laboratory studies in fully developed equilibrium flows (Hart *et al.*, 1996), suggesting that chemical signals entrained in natural habitats may not always be easily understood from currently available data.

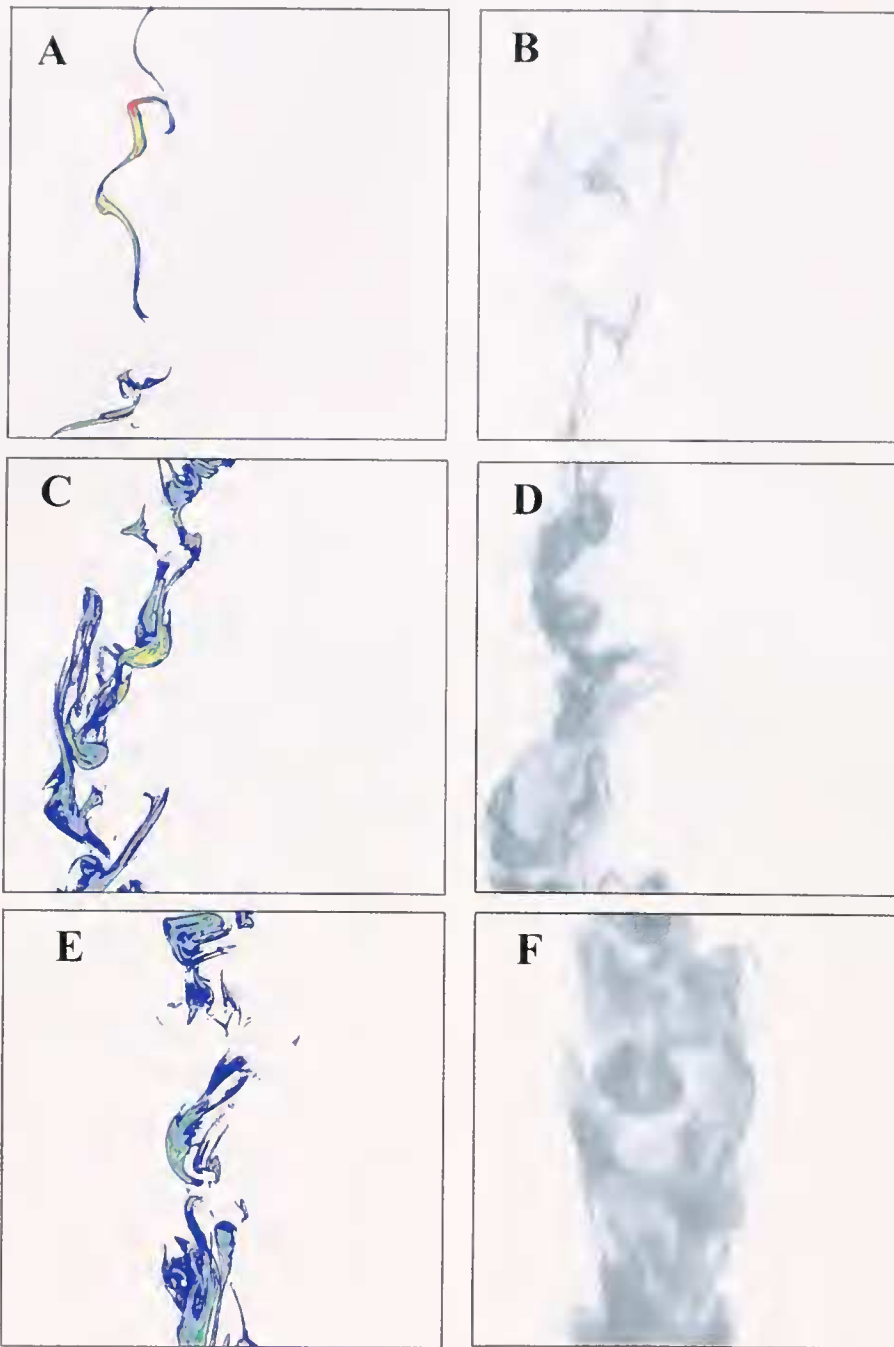
One problem that is difficult to circumvent is that most

open-channel flumes are rarely big enough to permit the large-scale meandering of the plume that is possible in less bounded natural habitats. The largest eddy size sustained in flume flows is on the order of the water depth (one reason why flumes must be much wider than deep—see Nowell and Jumars, 1987), which may or may not approximate the largest eddies in the field. These meanders induce a low-frequency component to the odor fluctuations, and hence could be of considerable importance to animals attempting to track plumes. These low-frequency components have not been well investigated in either the laboratory or the field. In addition to constraints imposed by flume geometry, the long temporal sampling necessary to capture these long-period components has not been performed, and obtaining the long-term records necessary to characterize larger scale plume movements should have high priority in future studies of plume dynamics.

Although flow fulfills a critical function for some animals in terms of specifying a general direction towards the source, investigators have suggested that it may be used for other purposes during orientation. It may, for instance, help steer an animal back into a plume (Weissburg, 1997). Alternatively, a coherent eddy containing odor may be a special cue due to the coincidence of information on both flow and odor. That animals may utilize this mechanism is suggested by the observations of Doall (discussed above) regarding mate-following in *Acartia hudsonica*, whereas Atema (1996) has speculated that larger animals may use such cues in a similar fashion.

If the co-occurrence of flow and odor is indeed part of the strategic repertoire of chemoperception, than its utility surely depends on the flow characteristics. In low *Re*, the two signals will be correlated for only as long as a vortex shed by an animal remains in motion. In *Temora longicornis*, vortices in the wake of a vigorously moving animal retain fluid motion for no more than 0.5 s (van Duren *et al.*, 1998). Thus, the receiver must be close to the source to have any likelihood of encountering the signal during the brief time that it contains both flow and odor information.

In high *Re* flows, the constraints on detecting coincident signals are quite different. Because of the energy (Kolmogorov) cascade, the fluid movements that create a given odor-containing eddy may subsequently transfer their energy to smaller length scales, leaving an odor signature that no longer reflects the fluid mechanical disturbances involved in its creation. Whether or not the superimposed patterns of velocity and odor concentration contain information is contingent on the strength of the correlation between velocity and odor fluctuations through both space and time. The integrity of chemical structures moving downstream in flow suggests that these two measures may be only loosely associated, but careful, simultaneous measurements of odor and velocity fluctuations are needed before a final conclusion is reached.



**Figure 4.** Paired laser-induced fluorescence (LIF) and dye visualization of an odor jet at different exit velocities. The left panels show LIF images, and the right panels show dye visualizations. All pictures were taken with a flow velocity of 5 cm/s, and the jet nozzle (2 mm i.d.) located 8 cm above the bottom, and pictures were taken at a distance of 60 cm downstream from the source using a concentration of rhodamine 6G equal to 200  $\mu\text{g/l}$ . Each pair of images represents the same flow conditions, although at different times, and the images were chosen to provide representative views of the odor at each flow regime. Images were false colored so that concentration increases from blue (lowest) to red (highest). (A-B) exit velocity 5 cm/s; (C-D) exit velocity 20 cm/s; (E-F) exit velocity 40 cm/s. When the release rate is isokinetic to the flow, the resulting odor signal is coherent, filamentous, and with local regions of high intensity. As jet velocity increases, the odor source becomes mixed more thoroughly and concentrations are lower, in spite of the increase in the amount of dye released. The field is approximately  $15 \times 15$  cm.

### Concluding Remarks

Sensory systems are adaptations to their signal environment, and behavioral responses to chemical signals must be considered in the context of the fluid mechanical structures that determine the spatial and temporal properties of odor cues. Across a broad span of different taxonomic groups, organisms in particular fluid regimes characterized by Re, Kolmogorov scales, and other basic fluid mechanical properties converge upon common strategies of locomotion and orientation.

Our studies of chemosensory orientation have reached a stage where comparisons across taxa, if properly phrased, present an exciting opportunity to attain a more precise understanding of sensory and behavioral mechanisms. To advance further, we must continue our trend of placing the animal firmly in its fluid mechanical environment and probing more finely the properties of fluid flow and signal structure that have significant impacts on locomotory performance. The framework for our investigations should be to draw appropriate linkages between animals that operate in similar or dissimilar environments. Do copepods and ants have functionally similar abilities? Has the seeming dynamic similarity between crabs and moths really resulted in equivalent strategies? Is it possible to gain insights into the orientation of midwater creatures through studies of bacterial chemotaxis? Our abilities to develop creative approaches to these questions will, in large measure, determine our progress in understanding the sensory ecology of chemoperception.

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